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ORIGINAL ARTICLE

# Assessing the trophic ecology of three sympatric squid in the marine ecosystem off the Patagonian Shelf by combining stomach content and stable isotopic analyses

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## ABSTRACT

Squid species are important components of the Southern Atlantic Ocean ecosystems, as they prey on a wide range of crustaceans, fish and cephalopods. As a result of this trophic interaction and their high abundance, they are considered reliable indicators of energy transfer and biomass in the food web. We identified *Illex argentinus*, *Doryteuthis gahi* and *Onykia ingens* as the most important squid species interacting on the Patagonian shelf, and used isotope analysis and stomach content identification to assess the feeding ecology and interaction of these squids in the ecosystem. Our results describe trophic interactions by direct predation of *O. ingens* and *I. argentinus* on *D. gahi*, and a trophic overlap of the three squid, and indicate a higher trophic level and differences in the foraging areas for mature and maturing *D. gahi* inferred through  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  concentrations. These differences were related to the segregation and different habitat of large mature *D. gahi* and suggest a food enrichment of C and N based on feeding sources other than those used by small maturing *D. gahi* and *I. argentinus* and *O. ingens*.

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## Introduction

Squid are important components of marine ecosystems (Coll et al. 2013) and their populations are extensively exploited by fisheries (Rodhouse & Nigmatullin 1996; Agnew et al. 2005; Portela et al. 2010; Rosas-Luis et al. 2014). The ommastrephid *Illex argentinus* (Castellanos, 1960), the loliginid *Doryteuthis gahi* (d'Orbigny, 1835) and the onychoteuthid *Onykia ingens* (E. A. Smith, 1881) are three squid species that coexist in the same oceanic areas, competing for available food resources. Similar to other squid, these species are short-lived terminal spawners (lifespan of 1–2 years) that exhibit high metabolic and growth rates, and feed voraciously on a wide range of prey (Rodhouse & Nigmatullin 1996; Rosas-Luis et al. 2014). In the Southern Ocean and off central and southern Patagonia, these three squid species are active predators of crustaceans, fish and molluscs (Rosas-Luis et al. 2014). Small squid feed exclusively on crustaceans; medium-sized individuals of *I. argentinus* and *O. ingens* feed on fish, molluscs and crustaceans; and larger squid feed on cephalopods and fish (Phillips et al. 2001, 2003a; Jackson et al. 1998; Cherel &

Duhamel 2003; Rosas-Luis et al. 2014). *Doryteuthis gahi* and *I. argentinus* are abundant species in the Patagonian Shelf ecosystem and are important prey of marine mammals, sea birds, pelagic fish and other squid (Ivanovic & Brunetti 1994; Cherel & Weimerskirch 1999; Mouat et al. 2001). The Patagonian Shelf is influenced by two currents: a northward flow of cold waters in the south – the Falklands/Malvinas Current (FC) – and the presence of warm-water eddies formed at the Brazil/Falkland/Malvinas Confluence (BFC) at around 38°S, causing high hydrographic mesoscale variability reflected in high primary production and a suitable area for squid (Palma et al. 2008).

Morphologically, mature individuals of the three species differ in body size, with *D. gahi* being the smallest (17 cm maximum mantle length), followed by *I. argentinus* (40 cm) and then *O. ingens* (50 cm) (Jackson et al. 1998; Phillips et al. 2003b; Crespi-Abril et al. 2009; Rodhouse et al. 2013; Rosas-Luis et al. 2014). The oceanic movements of *I. argentinus* and *O. ingens* are quite similar to other squid, migrating from the surface to deeper waters close to 500 m during the day (Moiseev 1991; Brunetti & Ivanovic 1992; Gilly et al. 2006; Watanabe et al. 2006). For

**Table 1.** Summary data of squid species and potential prey sampled over the Patagonian Shelf. Myctophids, amphipods and *Euphausia superba* values were taken from Wada et al. (1987), Dunton (2001), Cherel et al. (2002) and Corbiser et al. (2004).

Species	Depth (m)	ML (cm)	Sex (female, male)	Total	$\delta^{13}\text{C}$ (mean $\pm$ SD)	$\delta^{15}\text{N}$ (mean $\pm$ SD)	Trophic level
<i>Doryteuthis gahi</i> (d'Orbigny, 1835) (maturing)	285	8.9–10	8, 2	10	$-18.48 \pm 0.18$	$13.18 \pm 0.80$	5.05
<i>Doryteuthis gahi</i> (d'Orbigny, 1835) (mature)	285	23.5–27.5	10, 0	10	$-17.12 \pm 0.21$	$12.69 \pm 0.52$	4.93
<i>Illex argentinus</i> (Castellanos, 1960)	111–261	23.7–35.1	10, 10	20	$-18.92 \pm 0.47$	$11.98 \pm 0.97$	4.68
<i>Onykia ingens</i> (E. A. Smith, 1881)	168–285	24.9–37.1	13, 8	21	$-18.59 \pm 0.76$	$11.48 \pm 1.19$	4.52
<i>Munida gregaria</i> (Fabricius, 1793)				5	$-18.01 \pm 0.16$	$11.83 \pm 0.75$	4.63
<i>Patagonotothen</i> sp.				5	$-18.96 \pm 0.93$	$12.39 \pm 1.02$	4.8
<i>Micromesistius australis</i> Norman, 1937				1	$-18.47$	$11.66$	4.58
Amphipods					$-23.1$	$5.6$	2.68
Myctophids					$-21.8$	$8.4$	3.52
<i>Euphausia superba</i> Dana, 1850					$-28.78 \pm 1.37$	$3.15 \pm 0.60$	1.92

ML = mantle length, SD = standard deviation.

*D. gahi*, this vertical migration differs between adults and juvenile individuals; adult individuals are distributed near the surface, while juveniles and maturing adults perform diel vertical migrations to deep waters (Arkhipkin et al. 2013).

Rosas-Luis et al. (2014) described the trophic interactions between *D. gahi*, *I. argentinus* and *O. ingens* using traditional stomach content analyses for the central part of the Patagonian Shelf (the same fishing area in this study), a methodology that reflects the diet on a short-term scale (hours to a few days) in a particular place (Hyslop 1980). Stable isotopes of nitrogen (denoted as  $\delta^{15}\text{N}$ ) and carbon (denoted as  $\delta^{13}\text{C}$ ) have been increasingly used as an alternative and complementary tool to study the feeding behaviour of predators, including squid (McCutchan et al. 2003; Cherel & Hobson 2005; Navarro et al. 2013).  $\delta^{15}\text{N}$  values are indicators of a consumer's trophic position as the consumer's tissues become enriched in  $\delta^{15}\text{N}$  relative to their food (McCutchan et al. 2003; Vanderklift & Ponsard 2003). Variation in  $\delta^{15}\text{N}$  values in consumers may result not only from the trophic level at which they feed (Cherel et al. 2008), but also from changes at the base of the food web (Hobson & Cherel 2006); nevertheless latitudinal variation of  $\delta^{15}\text{N}$  is relatively low in oceanic waters of the Southern Ocean, and seasonal variation is integrated and buffered throughout the food web, from short-lived phytoplankton to long-lived predators (Cherel et al. 2008).  $\delta^{13}\text{C}$  values are mainly used to determine primary sources in a trophic network (McCutchan et al. 2003). In marine environments,  $\delta^{13}\text{C}$  values indicate the inshore/pelagic versus offshore/benthic contribution to food intake (Hobson et al. 1994; Cherel & Hobson 2007; Navarro et al. 2013). In the giant squid *Architeuthis dux* Steenstrup, 1857, the more positive  $\delta^{13}\text{C}$  values indicate the use of waters to the north of the subtropical front to the Kerguelen waters in Southern Oceans (Cherel & Hobson, 2005), and for *O. ingens*,  $\delta^{13}\text{C}$  values suggest that this species lives essentially in the same water mass throughout its life (Cherel &

Hobson 2005). The combination of both stomach contents and isotopic analyses results in a better understanding of the feeding ecology and ecological role of marine organisms (see examples in Ruiz-Cooley et al. 2006; Connan et al. 2014; Navarro et al. 2014; Albo-Puigserver et al. 2015).

Considering their ecological importance as prey and predators in the ecosystem of the Patagonian Shelf, we analysed the feeding ecology (diet and trophic position) and trophic relationships between *D. gahi*, *I. argentinus* and *O. ingens*. Our analyses include the use of isotopic methodology corroborated with traditional stomach content analysis.

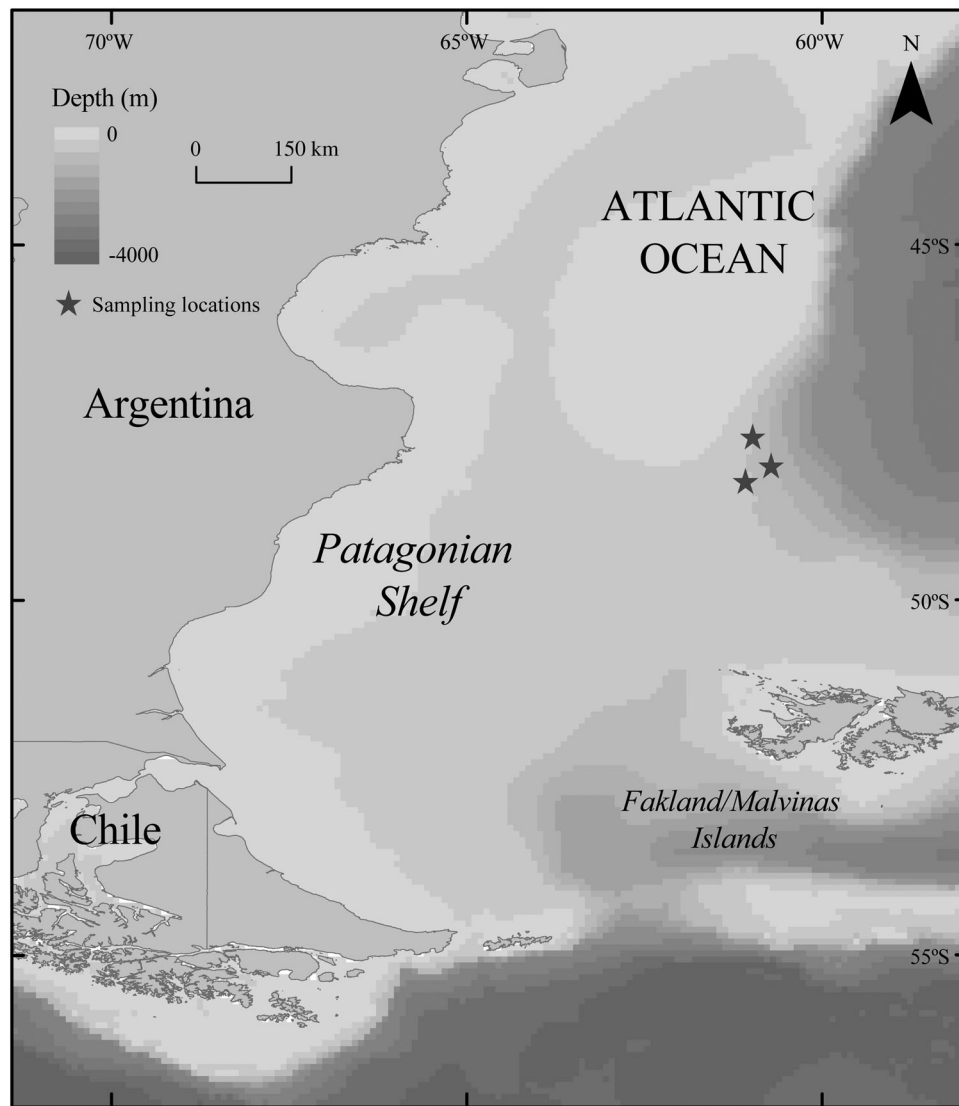
## Materials and methods

### Study area and sampling procedures

All specimens were captured by two commercial Spanish bottom-trawling vessels (C/V *Figaro* and C/V *Manuel Ángel Nores*) over the Patagonian Shelf between 6 and 8 May 2013 at depths between 111 and 285 m using a four-panel trawl of 64.40  $\times$  84.85 m (Table 1, Figure 1). Stomach content and stable isotope analyses were carried out on *Doryteuthis gahi*, *Illex argentinus* and *Onykia ingens*. Each specimen was immediately frozen on board after capture and stored at  $-20^\circ\text{C}$  until their morphological, stomach content and tissue isotopic analyses were conducted. Mantle length (ML) and body weight (BW) were recorded for all individuals as well as sex and maturity stage in three groups: immature, maturing and mature, according to Lipinski & Underhill (1995).

### Stomach content analysis

The stomachs of all individuals were extracted after dissection. Each stomach was weighed with a digital balance to determine the stomach content weight (SCW) and fullness weight index  $\text{FWI} = (\text{SCW} \times 100) /$



**Figure 1.** Southwestern Atlantic Ocean and sampling locations (black stars) of *Doryteuthis gahi*, *Illex argentinus* and *Onykia ingens*.

(BW–SCW), following Rasero et al. (1996), where BW is the body weight.

Stomach contents were identified under a binocular microscope (60–120×) to aid identification and all prey items were weighed to the nearest 0.01 g. Fish sagittal otoliths were identified using the parameters provided by Smale et al. (1995) and Lombarte et al. (2006). Cephalopod beaks were identified following Clarke (1986) and Xavier & Cherel (2009). Crustaceans were identified by their exoskeletons based on by Stebbing (1888) and Boschi et al. (1992).

Although the number of stomachs was low, we calculated the trophic indices to make comparisons with the results obtained with the isotopic mixing models and with the diet information reported in previous diet studies. Frequency of occurrence and numeric and

gravimetric methods were used to quantify the diet. Frequency of occurrence (%FO) was calculated as the percentage of squid that fed on a certain prey  $\%FO = (n_i / N) * 100$ , where  $n_i$  is the number of stomachs with prey  $i$ , and  $N$  is the total number of stomachs containing prey. The numeric method (%N) is the number of individuals of a certain prey ( $p_i$ ) relative to the total number of individual prey ( $P$ ) as follows:  $\%N = (p_i / P) * 100$ . The gravimetric method (%W) is defined as the weight of a certain prey ( $w_i$ ) relative to the total weight of all prey ( $W$ ), as follows:  $\%W = (w_i / W) * 100$ , (Cailliet 1976). The index of relative importance (IRI) was calculated following Pinkas et al. (1971):  $IRI = (\%N + \%W) * (\%FO)$ . The IRI was expressed as:  $\%IRI = (IRI / \sum IRI) * 100$ , and compared with those previously reported by Rosas-Luis et al. (2014) for the same area and same species.

### Stable isotopic analysis

A small portion of mantle was extracted from each individual. All samples were freeze-dried and powdered, and 0.270–0.300 mg of each sample was packed into tin capsules. Isotopic analyses were performed at the Laboratory of Stable Isotopes at the Estación Biológica de Doñana. Samples were heated to 1020°C using a continuous flow isotope-ratio mass spectrometer (Thermo Electron) by means of a Flash HT Plus elemental analyser interfaced with a Delta V Advantage mass spectrometer. Stable isotope ratios were expressed in the standard  $\delta$ -notation (‰) relative to Vienna Pee Dee Belemnite ( $\delta^{13}\text{C}$ ) and atmospheric  $\text{N}_2$  ( $\delta^{15}\text{N}$ ). Based on laboratory standards, the measurement error was  $\pm 0.1$  and  $\pm 0.2$  for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively. The C:N ratio of all tissues was always lower than 3‰, and hence no correction of the  $\delta^{13}\text{C}$  values was required to account for the presence of lipids (Logan et al. 2006). To compare the isotope results, four groups of squid were defined: one for immature *Doryteuthis gahi*, one for mature *D. gahi*, one for *Illex argentinus*, and one for *Onykia ingens* (Table I). ANOVA and post-hoc Tukey tests were used when comparing isotope values between groups.

### Trophic level

The trophic level position of each squid and prey species was calculated according to Cherel et al. (2008) and Braid & Bolstad (2014), using the following equation:

$$\text{TL} = [(\delta^{15}\text{N}_{\text{squid or prey}} - 3.4) - 3.2^{-1}] + 2,$$

where TL is the trophic level of that consumer,  $\delta^{15}\text{N}_{\text{squid or prey}}$  represents the values of the consumer's muscle tissue; 3.4 is the mean  $\delta^{15}\text{N}$  for *Salpa thompsoni* Foxton, 1961 (in ‰) with a trophic level of 2 according to Perissinotto & Pakhomov (1998), and 3.2 is the average trophic enrichment factor (Sweeting et al. 2007).  $\delta^{15}\text{N}$  values of the squat lobster *Munida gregaria* (Fabricius, 1793) ( $n = 5$  samples), the longtail southern cod *Patagonotothen ramsayi* (Regan, 1913) ( $n = 5$ ) and the southern blue whiting *Micromesistius australis* Norman, 1937 ( $n = 1$ ), were calculated based on samples collected with the same trawl net and at the same time as the squid. The  $\delta^{15}\text{N}$  values of *Euphausia superba* Dana, 1850, amphipods and myctophids were taken from previous studies (Wada et al. 1987; Dunton 2001; Cherel et al. 2002; Corbiser et al. 2004).

### Isotopic mixing model

To evaluate the relative contributions of the different food sources, based on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotopic

signatures of the four groups of squid (maturing and mature *Doryteuthis gahi*, *Illex argentinus* and *Onykia ingens*), a Bayesian stable isotope mixing model was implemented in the software package SIAR (Stable Isotope Analysis in R) (Parnell et al. 2010). The model considers a transfer energy factor of  $3.4 \pm 1$  for  $\delta^{15}\text{N}$ , and  $0.4 \pm 1.3$  for  $\delta^{13}\text{C}$ , which allows the inclusion of isotopic signatures and fractionation together with the uncertainty of these values within the model. We used the same isotopic enrichment values used to calculate the trophic level. Isotope niche metrics (Bayesian ellipse area) and trophic overlap between species were also calculated using the SIAR package (Jackson et al. 2011). These analyses use measurements based on ellipses calculated by a covariance matrix that defines their shape and area, and values close to 1 represent high trophic overlap (Jackson et al. 2011). The ellipse area was proposed as an unbiased metric with respect to sample size and, particularly for the Bayesian method, which incorporates greater uncertainty with smaller sample sizes, resulting in larger ellipse areas (Jackson et al. 2011). Both methods were fitted using R 3.1.0 for Windows (R Development Core Team 2014). Three potential prey groups were selected for the isotopic mixing models based on the feeding habits reported in this study and those of Rosas-Luis et al. (2014): crustaceans (*Euphausia superba*, amphipods and *Munida gregaria*), fish (*Patagonotothen* sp., myctophids and *Micromesistius australis*), and squid (*Doryteuthis gahi*, *Illex argentinus*); *Onykia ingens* was not considered as a prey group as it was not identified in the stomach contents of the three squid (Table I).

## Results

### Stomach content results

Ten muscle samples of maturing and 10 mature *Doryteuthis gahi*, 20 of *Illex argentinus* and 21 of *Onykia ingens* were used in the isotopic analysis. All the stomachs were analysed for the identification of prey, except for *O. ingens* for which only 17 stomachs contained food items.

Maturing *Doryteuthis gahi* fed on crustaceans, *Euphausia* sp. and *Themisto gaudichaudii* Guérin, 1825, while mature *D. gahi* fed on fish and the squat lobster *Munida gregaria* (Table II). In contrast, the diet of *Illex argentinus* was composed of fish, with *Arctozenus risso* (Bonaparte, 1840) and *Patagonotothen ramsayi* (Regan, 1913) being the most important, and crustaceans, with *T. gaudichaudii* being the most important (Table III). *Illex argentinus* also included the squid *D. gahi* and *I. argentinus* in their diet.



**Table II.** Percentages of the number N, weight W, frequency of occurrence FO, and the index of relative importance IRI of the feeding resources for 10 maturing and 10 mature *Doryteuthis gahi*. UN is unidentified.

Prey	<i>D. gahi</i> maturing				<i>D. gahi</i> mature			
	%N	%W	%FO	%IRI	%N	%W	%FO	%IRI
Chordata								
Actinopterygii UN	6.25	0.05	10.00	0.41	42.90	60.70	30.00	67.72
Crustacea	93.75	99.94	80.00	99.59	28.60	37.60	20.00	28.84
Decapoda								
Amphipoda								
<i>Themisto gaudichaudi</i> Guérin, 1825	43.75	0.53	29.86	28.27				
Unidentified	6.25	5.29	10.00	1.47				
Euphausiacea								
<i>Euphausia</i> sp.	43.75	64.79	50.00	69.45				
Munididae								
<i>Munida gregaria</i> (Fabricius, 1793)					28.60	37.60	20.00	27.96
Teuthida UN					14.30	1.53	10.00	3.34
Cnidaria (Cubozoa)					14.30	0.13	10.00	3.05

Similar to *I. argentinus*, the diet of *O. ingens* was mainly composed of fish, with *Lampanyctus australis* Tåning, 1932, *Notoscopelus* sp., *Micromesistius australis* and *Notophycis marginata* (Günther, 1878) being the most important, followed by squid, with *Histioteuthis* sp., *Histioteuthis atlantica* (Hoyle, 1885) and *D. gahi* identified in the stomach contents (Table III).

### Isotopic results and SIAR outputs

The analysis of variance (ANOVA test) of  $\delta^{13}\text{C}$  values yielded significant differences between the three squid ( $F_{1,59}=48.18$ ,  $P < 0.05$ ). A post-hoc Tukey test showed that maturing *Doryteuthis gahi*, mature *D. gahi* and *Illex argentinus* differed significantly at  $P < 0.05$  (Table I and IV), and that mature *D. gahi* and *Onykia ingens* differed significantly at  $P < 0.05$  (Table I and IV).  $\delta^{15}\text{N}$  values also differed between the three squid ( $F_{1,38} = 8.26$ ,  $P < 0.05$ ).

Regarding the standard elliptic areas (SEA) (Figure 2), we found that *O. ingens* showed the highest values (SEA = 1.44), followed by *I. argentinus* (SEA = 1.30), maturing *D. gahi* (SEA = 0.52) and mature *D. gahi* (SEA = 0.39). We also found an overlap between the SEA of *O. ingens*, *I. argentinus* and maturing *D. gahi* (Figure 2). The highest SEA overlap was found between *O. ingens* and *I. argentinus* (SEA overlap = 0.52), followed by *I. argentinus* and maturing *D. gahi* (SEA overlap = 0.12), and maturing *D. gahi* and *O. ingens* (SEA overlap = 0.05). In contrast, the SEA of mature *D. gahi* was segregated from the other groups (Figure 2B).

Regarding trophic level based on  $\delta^{15}\text{N}$  values, we found that *D. gahi* showed the highest trophic level (TL = 5.05), followed by *I. argentinus* (TL = 4.68) and *O. ingens* (TL = 4.52). *Munida gregaria* ( $\delta^{15}\text{N} = 11.83 \pm 0.75$ , TL = 4.63), *Patagonotothen* sp. ( $\delta^{15}\text{N} = 12.39 \pm 1.02$ , TL = 4.80) and *Merluccius australis* (Hutton, 1872)

( $\delta^{15}\text{N} = 11.66$ , TL = 4.58) were at similar trophic levels to *I. argentinus* and *O. ingens*. *Euphausia superba* ( $\delta^{15}\text{N} = 3.15 \pm 0.60$ , TL = 1.92) showed the lowest trophic level (Table I).

SIAR results indicated that fish and squid were the main prey groups for the three squid species studied (Figure 3), with the proportion of fish higher than crustaceans for maturing *D. gahi* individuals.

### Discussion

We found that the squid *Doryteuthis gahi*, *Illex argentinus* and *Onykia ingens* on the Patagonian Shelf exploit similar feeding resources (fish, crustaceans and squid) as indicated by previous results (Ivanovic & Brunetti 1994; Santos & Haimovici 1997; Jackson et al. 1998; Mouat et al. 2001; Phillips et al. 2001, 2003a, 2003b; Arkhipkin & Middleton 2002; Cherel & Duhamel 2003; Ivanovic 2010; Rosas-Luis et al. 2014). Previous reports were based on traditional stomach content analysis of squid caught by trawl nets, which appear to be reliable indicators of the feeding habits of these squid. The method of capture of these squid (trawling in the present study and jig-caught for other studies) may lead to a misinterpretation of feeding components because the squid can actively feed on prey also present in the fishing net (Ibañez et al. 2008). However, in order to reduce the identification bias and fish consumed inside the trawl net, we used hard structures, such as fish otoliths and cephalopod beaks that remain after a lengthy period of digestion. Considering that all studies reported a similar feeding composition of the dietary habits of these three species, we incorporated the isotope analysis to explain the trophic ecology based on the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of the three squid. For this reason, the stomach content results were only used to confirm the feeding component with previous reports (Rosas-Luis et al.

**Table III.** Percentages of the number N, weight W, frequency of occurrence FO, and the index of relative importance IRI of the feeding resources for 20 *Illex argentinus* and 17 *Onykia ingens*. UN is unidentified.

Prey	<i>I. argentinus</i>				<i>O. ingens</i>			
	%N	%W	%FO	%IRI	%N	%W	%FO	%IRI
Chordata								
Actinopterygii	26.31	34.86	75.00	55.45	63.82	82.70	58.82	81.27
Gadidae								
<i>Micromesistius australis</i> Norman, 1937					4.25	0.96	5.88	1.36
Paralepididae								
<i>Arctozenus risso</i> (Bonaparte, 1840)	1.75	1.44	5.00	0.27				
Myctophidae								
<i>Lampanyctus australis</i> Tåning, 1932					40.43	24.51	5.88	16.98
<i>Notophycis marginata</i> (Günther, 1878)					4.25	1.27	5.88	1.44
<i>Notoscopelus</i> sp.					2.13	46.32	5.88	12.67
Unidentified	1.75	3.96	5.00	0.49				
Notothentidae								
<i>Patagonotothen ramsayi</i> (Regan, 1913)	1.75	4.48	5.00	0.53				
Actinopterygii UN	21.05	24.98	60.00	47.20	12.76	9.63	35.29	35.13
Crustacea	66.66	24.28	30.00	32.97	12.76	8.77	35.29	7.16
Amphipoda								
<i>Themisto gaudichaudi</i> Guérin, 1825	64.91	24.28	30.00	45.73				
Amphipoda UN					2.13	0.33	5.88	0.64
Euphausiacea								
<i>Euphausia</i> sp.	1.75	0.01	5.00	0.15				
Munididae								
<i>Munida</i> sp.					6.38	0.01	17.64	5.02
<i>Munida gregaria</i> (Fabricius, 1793)					4.26	8.42	11.76	6.63
Mollusca	7.01	40.85	20.00	11.57	21.27	8.49	41.17	11.56
Cephalopoda								
Teuthida								
Histioteuthidae								
<i>Histioteuthis</i> sp.					8.51	1.99	17.65	8.24
<i>Histioteuthis atlantica</i> (Hoyle, 1885)					2.13	0.08	5.88	0.58
Loliginidae								
<i>Doryteuthis gahi</i> (d'Orbigny, 1835)	3.51	14.40	10.00	3.06	2.13	0.72	5.88	0.74
Ommastrephidae								
<i>Illex argentinus</i> (Castellanos, 1960)	1.75	0.08	5.00	0.16				
Teuthida UN	1.75	26.38	5.00	2.40	6.38	5.64	17.65	9.43
Cephalopoda UN					2.13	0.06	5.88	0.57
Phaeophyta					2.13	0.03	5.88	0.56

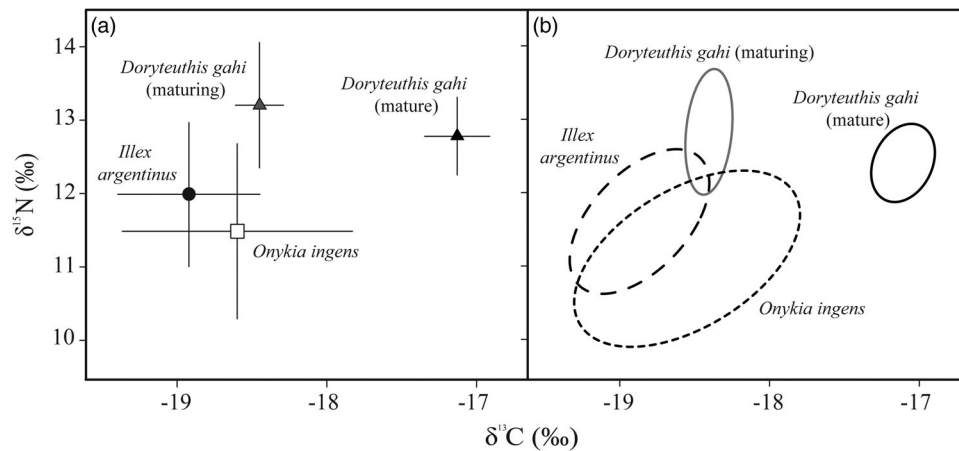
2014). The combination of the two methodologies, stomach content and isotopic values, provides new ways of quantifying the trophic ecology and relationships between squid, which we present in this study.

An evident segregation in the  $\delta^{13}\text{C}$  values between mature *D. gahi* and the other squid was found, probably reflecting the different use of benthic/inshore vs pelagic/offshore waters between them (Hobson &

Welch 1992). Mature *D. gahi* showed high  $\delta^{13}\text{C}$  values, indicating its pelagic, shallow and neritic feeding habits, and confirmed the inshore spawning migration of mature *D. gahi* (Hobson et al. 1994; Arkhipkin et al. 2004, 2013; Cherel & Hobson 2007). On the other hand, maturing *D. gahi*, *I. argentinus* and *O. ingens* showed more negative  $\delta^{13}\text{C}$  values that are coincident with the active vertical migrations in oceanic and deep waters of maturing *D. gahi* and *I. argentinus* (Arkhipkin et al. 2013), and with *O. ingens* which lives and feeds primarily in deep waters (Cherel & Hobson 2005). The enrichment of  $\delta^{13}\text{C}$  values related to different foraging areas of mature *D. gahi* is similar to those reported by Cherel et al. (2008) in the southern ocean where the elephant seal feeds in open oceanic waters (low  $\delta^{13}\text{C}$  values) and the gentoo penguin *Pygoscelis papua* (Forster, 1781) feeds in neritic waters (high  $\delta^{13}\text{C}$  values). Nonetheless, the  $\delta^{13}\text{C}$  value for mature *D. gahi* is enforced with the inclusion of the squat lobster *Munida gregaria* (TL = 4.63) as their main prey item. The maturity stage of *M. gregaria* was not identified in our samples but

**Table IV.** Results of the post-hoc Tukey test of *Doryteuthis gahi*, *Illex argentinus* and *Onykia ingens*.

Group	Group	$\delta^{15}\text{N}$ (P-value)	$\delta^{13}\text{C}$ (P-value)
<i>D. gahi</i> (d'Orbigny, 1835) maturing	<i>I. argentinus</i>	<0.05	<0.05
	<i>O. ingens</i>	0.62	<0.05
	<i>D. gahi</i> mature	<0.05	0.80
<i>D. gahi</i> (d'Orbigny, 1835) mature	<i>D. gahi</i> maturing	<0.05	0.80
	<i>I. argentinus</i>	<0.05	0.17
	<i>O. ingens</i>	<0.05	<0.05
<i>Illex argentinus</i> (Castellanos, 1960)	<i>D. gahi</i> maturing	<0.05	<0.05
	<i>O. ingens</i>	0.20	0.35
	<i>D. gahi</i> mature	<0.05	0.17
<i>Onykia ingens</i> (E. A. Smith, 1881)	<i>D. gahi</i> maturing	0.62	<0.05
	<i>I. argentinus</i>	0.20	0.35
	<i>D. gahi</i> mature	<0.05	<0.05



**Figure 2.** (A) Mean  $\pm$  standard deviation of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values in muscle of *Doryteuthis gahi*, *Illex argentinus* and *Onykia ingens*; (B) isotopic standard ellipses of each squid species.

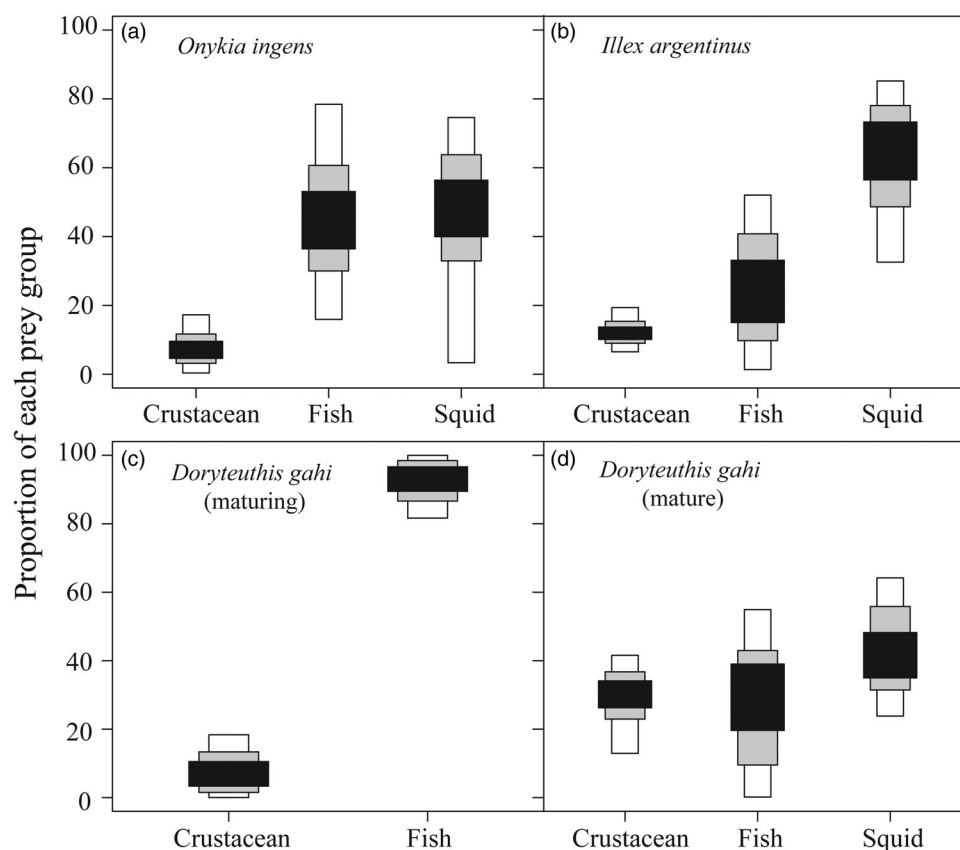
juveniles of this species are known to be pelagic, forming dense aggregations in shallow waters (Ravilli et al. 2010) where they are available to be preyed upon by mature *D. gahi*. This result suggests that mature *D. gahi* are moving in and out of the distribution area of maturing *D. gahi*, a result that is corroborated by the period in which the samples were collected. Samples were collected in May, which coincides with the start of one of the two reproductive periods of *D. gahi* (May to July) when both mature and maturing groups are interacting in the same area (Arkhipkin et al. 2004, 2013).

$\delta^{15}\text{N}$  values indicated that these three squid are placed at high trophic levels (TL= 4.5 to 5). These results agree with the known trophic web of squid based on fish, squid and large crustaceans (Ivanovic & Brunetti 1994; Santos & Haimovici 1997; Jackson et al. 1998; Mouat et al. 2001; Phillips et al. 2001, 2003a, 2003b; Arkhipkin & Middleton 2002; Cherel & Duhamel 2003; Ivanovic 2010; Rosas-Luis et al. 2014) and with the assumption that the highest  $\delta^{15}\text{N}$  values are related to the trophic level of prey and the ontogenetic growth of predators (DeNiro & Epstein 1981; Vanderklift & Ponsard 2003; Newsome et al. 2009; Navarro et al. 2011) resulting in a reliable description of the feeding activity of mature *D. gahi*, *I. argentinus* and *O. ingens* (Hatfield & Rodhouse 1994). Trophic levels of mature *D. gahi*, *I. argentinus* and *O. ingens* were determined from the consumption of food sources with a trophic level of 1.9 to 4.8 (euphausiids, myctophids, other fish and squid) (Rosas-Luis et al. 2014), but contrasted with the average  $\delta^{15}\text{N}$  values of maturing *D. gahi* that resulted in the highest trophic level (trophic level = 5.05), with euphausiids and amphipods as main prey items according to the stomach content analysis. The difference in the TL of maturing and mature *D. gahi* is

related to the incorporation of prey such as *M. gregaria* with higher trophic levels of 4.6 in the feeding habits of mature *D. gahi*, and unidentified fish for maturing *D. gahi* (estimated prey contribution isotopes). Currently, stomach content and isotope analyses do not show the same results for maturing *D. gahi*. Thus, we suggest that the  $\delta^{15}\text{N}$  values of maturing *D. gahi* are affected by vertical movements of the feeding groups between 0 and 150 m depths, and horizontal movements in and offshore, promoting predation on prey other than those reported for *I. argentinus* and *O. ingens* (Ivanovic & Brunetti 1994; Phillips et al. 2001; Cherel & Duhamel 2003; Phillips et al. 2003a, 2003b). Unfortunately, there was a high number of unidentified fish in the stomach contents of *D. gahi* in this work and that previously reported by Rosas-Luis et al. (2014), suggesting that the stomach content identification in *D. gahi* does not reflect the  $\delta^{15}\text{N}$  enrichment in muscular tissue based on fish (Newsome et al. 2009), and that maturing *D. gahi* do not regularly consume crustaceans. Thus, systematic and molecular methods should be used to complete the description of the annual cycle of the feeding habits of this squid.

Finally, our results indicate that the use of complementary methodologies provides important information for a more thorough understanding of the trophic ecology of *D. gahi*, *I. argentinus* and *O. ingens*. Although isotopes do not typically reveal detailed information on dietary composition, the use of both methods offers a proxy for dietary variation between maturing and mature *D. gahi*, and between mature *D. gahi*, *I. argentinus* and *O. ingens*. These dietary patterns are characterized by an inshore-offshore ontogenetic migration of *D. gahi* inhabiting different areas and preying on feeding resources that are different from those of *I. argentinus* and *O. ingens*.





**Figure 3.** Results of the SIAR model (95-black boxes, 75-grey boxes and 50%-white boxes showing credibility intervals) showing estimated prey contributions to the diet of (A) *Onykia ingens*, (B) *Illex argentinus*, (C) *Doryteuthis gahi* (maturing) and (D) *Doryteuthis gahi* (mature), based on mantle isotopic values.

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